



Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

CHROMOSOME STUDIES ON THE DIPTERA. IV.
INCOMPLETE SYNAPSIS OF CHROMOSOMES
IN *DASYLLIS GROSSA* FABR.

C. W. METZ,

CARNEGIE INSTITUTION OF WASHINGTON, DEPARTMENT OF GENETICS.

INTRODUCTION.

In the robber fly, *Dasyllis grossa*, synapsis of chromosomes in spermatogenesis (and possibly in oögenesis) appears to be partially inhibited, in such a manner that three of the pairs of chromosomes undergo synaptic association for only a portion of their length. The behavior is relatively uniform and constant in these particular chromosomes and indicates that different regions of a chromosome behave differently as regards synapsis. The present account deals primarily with this feature of chromosome behavior and with its possible bearing on cases of abnormal cross-over values in genetical experiments with *Drosophila*.

The description of spermatogenesis is taken largely from one specimen of *D. grossa* Fabr., kindly identified by Mr. C. W. Johnson; but it applies in a general way to all of the *Dasyllis* material I have studied (a dozen or more specimens, representing *D. grossa* Fabr., *D. thoracica* Fabr., and probably two or three more species). I am not certain that all of these agree in detail, but each one shows indications of incomplete synapsis in one or more pairs of chromosomes.

Dasyllis provides particularly favorable material for a study of chromosome behavior during spermatogenesis, because of the small number and relatively large size of the chromosomes; the large size of the nuclei; the relatively enormous number of cells present; representing all stages from early spermatogonia to spermatozoa; and particularly the serial orientation of successive stages throughout the tubular testes, making it easy to trace the chromosome behavior step by step through the growth period. In addition, it should be mentioned that there is no contraction or synizesis stage, and no true "diffuse" stage when the chromatin can not be seen.

In its general features spermatogenesis in *Dasyllis* resembles that in *Asilus sericeus*, as described by Metz and Nonidez ('21), and no attempt will be made to give a complete account here. The technique employed in the present work was the same as that described in the preceding paper. The material was fixed in strong Flemming and stained in Heidenhain's iron hæmatoxylin.

Dasyllis is unique among the Diptera thus far studied in possessing an unpaired X-chromosome in the male. This is true of all the material I have studied in the genus. The other Diptera have all been of the X-Y type. In an earlier paper (Metz, '16, p. 243) *Dasyllis* was tentatively considered to possess a Y-chromosome, but additional material has shown clearly that no Y is present unless it is so minute as to be practically invisible.

I am indebted to Miss M. S. Moses for assistance in the laborious work of examining the ovaries in connection with the observations on oögenesis, and to Miss Ruth Lincks for making the drawings for the accompanying figures.

SPERMATOGONIA.

The spermatogonial chromosome group of *D. grossa* consists of three pairs of V-shaped and one pair of J-shaped (atelomitic) autosomes, and the unpaired X, as shown in Fig. 1. The J-shaped pair appears straight in this figure, but in later metaphases its subterminal spindle fiber attachment is evident. The V-shaped pairs are of different sizes, the smallest being readily distinguishable from the other two. Thus the X and two of the autosome pairs may be identified individually.

As in all of the other Diptera that I have studied, the paired association of chromosomes is persistent through successive spermatogonial generations, and into the final spermatogonial anaphase. In spermatogonial prophase (Figs. 2 and 3) the pairing of the large chromosomes does not seem to be as intimate medially as in most other flies—a fact which suggests that the peculiar repulsion or lack of attraction exhibited in the growth period is existent here also.

THE SPERMATOCYTE GROWTH PERIOD.

In *Dasyllis* the spermatocyte nucleus is relatively large at the beginning of the growth period; and partly on this account, per-

haps, the growth period does not involve an increase of more than about 30–50 per cent. in nuclear diameter.

The description of the growth period may best be taken up at a point shortly after growth has begun (returning later to a consideration of the earliest stages). At this time the chromosomes, with the exception, of the condensed X-chromosome, are in the form of long, deeply staining threads, closely applied to the nuclear membrane. There are four pairs of threads, in one of which (apparently the smallest) the two members are usually closely associated throughout their length—*i.e.*, the synaptic association is complete. In each of the other three the association is evident at each end but toward the middle the two components diverge to form large loops. Each pair of threads is very long, frequently extending more than half way around the circumference of the nucleus, hence it is practically impossible to represent them all in one figure. Individual pairs, however, are shown in Figs. 7 to 10. Most of these are complete, but in some (*e.g.*, Fig. 9) one or both ends of a pair may be cut off. To one of the three looped pairs (apparently the largest) is attached a large dense body (Fig. 7), which serves to identify this pair throughout the entire growth period. This body (see page 258 for description) is attached to both members of the pair in the looped region and normally lies at a point near one end of the loop—a position which it occupies with surprising regularity.

The three large pairs of chromosomes at this stage give the appearance of having undergone synapsis only near their ends—the threads having remained well apart medially for about one third to one half their length. In the smallest pair, as noted above, synapsis is usually complete, but in a few cases a small loop is present. The chromosome on the left in Fig. 9 appears to be such a case. Throughout the remainder (80 per cent. or more) of the growth period the condition of the chromosomes is maintained with relatively little change. The cells and nuclei grow somewhat and the chromosomes become more condensed and hence more easily examined. The X-chromosome remains condensed throughout. Successive stages are represented by thousands of cells and the transformation during growth is so gradual that scarcely any change is observable from one cyst to another down

the testis. It seems certain, therefore, that no important stage has been overlooked in this region.

Figs. 11 and 12 represent entire, or almost entire, nuclei showing the condition maintained by the chromosomes up to the end of the growth period. In each of the three large pairs of chromosomes the two components diverge medially in the form of a loop; while in the shorter pair they are usually closely applied throughout their length, with only occasionally a small loop visible. In Fig. 11 the entire contents of the nucleus are drawn in position; in Fig. 12 the pairs are transposed to facilitate examination, but are all taken from the same nucleus.

During the late prophase, as the chromosomes are about to go on the spindle, they become so condensed and shortened that in many cases the loops become closed (Fig. 13). The line of separation between the two chromosomes, however, is still evident, and it is practically certain that no intimate association occurs here.

It appears, then, that in the case of the three large pairs of chromosomes synapsis has been incomplete, unless it occurred at a very early stage in the growth period and was followed by a secondary opening out to form the loops. The evidence from the early stages may now be examined from this point of view.

THE EARLY GROWTH PERIOD.

The early growth stages resemble those of *Asilus sericeus* (Metz and Nonidez, '21) in a general way, but the details differ materially. In *Asilus* homologous chromosomes become closely associated in the final spermatogonial telophase and remain thus as they draw out into threads. Just before they draw out (stage *b*) the pairs look like single chromosomes relatively clear cut in outline. In *Dasyllis* the chromosomes are likewise paired; but the pairs form loose, irregularly granulated aggregates, giving little or no indication of the intimate association seen in *Asilus*.

The aggregates become more loose and irregular in structure as growth proceeds, and then draw out into irregular, granulated threads. Only two bodies remain condensed: one the X-chromosome and the other the "dense body" attached to the large pair of chromosomes. As the aggregates spin out into threads a more intimate association becomes possible. Unfortunately as the spin-

ning out proceeds the threads become entangled and lose much of their staining capacity, making this the most difficult stage to analyze. In fact, it is impossible to trace all of the chromosomes in any one nucleus. It is significant, however, that as soon as the aggregates have elongated two kinds of threads may be observed: single and double; and occasionally in favorable nuclei the two members of a double one may be seen to diverge in the form of a Y, or may even form a loop essentially like those of later stages. The most convincing evidence as to the nature of events at this time is obtained from an examination of the threads attached to the "dense body." As has been noted above, this body in later stages is attached to the two single threads making the loop in one of the large chromosome pairs. By following this structure through the early stages, then, it should be possible to determine whether or not the loop is present here also. A careful study of this feature has convinced me that the loop is normally present throughout the early stages—from the time the chromosomes first elongate. In some cases the entire structure may be seen, as shown in Figs. 4 and 6, and in others it is evident that the threads running out from the dense body are single, not double. The fact that single threads and occasionally loops (Fig. 5) may also be seen in other parts of the nucleus makes it seem almost certain that the same conclusion applies to the other large chromosomes. It is practically impossible to differentiate the smallest chromosome pair from the others in the early stages, hence I have been unable to determine whether or not it possesses a loop at this time. A little later the chromosome pairs move to the periphery of the nucleus and become separated sufficiently to permit of individual analysis—which brings them into the stage with which our description began (Figs. 7 to 9).

It is possible, of course, to assume that the chromosome pairs do not behave synchronously in the very early stages, and to imagine them undergoing, one at a time, a complete synapsis followed immediately by a partial opening out into loops. This would account for the constant presence of both single and double threads in the nucleus. Such an explanation seems improbable, however, from analogy with other forms, and especially in view of the evidence furnished by the chromosome pair attached to the

dense body, which may be traced through all the stages. The conclusion seems justified, therefore, that synapsis does not occur in the looped regions of the three large chromosome pairs.

THE "DENSE BODY."¹

This body, which appears to take the place of the nucleolus in other flies, has such a consistent connection with one of the large pairs of chromosomes throughout the growth period that its structure and history may be considered in some detail. It is usually ovoid or spherical, deeply staining in iron hæmatoxylin, and clear cut in outline. In some cases it is clearly bipartite in structure, and rarely it is divided into entirely separate parts. As already noted, it is attached to both members of one of the large chromosome pairs, probably the J-shaped pair. When it is divided into two parts, as in Figs. 17 to 19, this independent attachment is shown clearly. Associated with the dense body, on the side opposite the attachment to the chromosomes, is an achromatic structure (presumably a plasmosome), of variable size and irregular outline, as shown in Figs. 11, 12, and 18.

The origin of the dense body can not be traced accurately enough to demonstrate that it arises directly and equally from the two members of the one pair of chromosomes, but its subsequent history (attachment, bipartite structure, behavior in late prophase) suggests such an origin.

During the prophase of the first spermatocyte division, as the chromosomes go on the spindle, the dense body diminishes in size. It gives the appearance of being taken up, in part at least, by the attached chromosomes, for there is little indication of any of it diffusing or breaking off. It separates into two components at this time, coincident with the separation of the two chromosomes (Figs. 20, 21) preparatory to the reduction division. They persist in this condition up to, and perhaps through, the metaphase, as do the somewhat similar "chromosome vesicles" observed by Carothers ('13) in the Orthoptera *Brachystola* and *Arphia*. I have not attempted to follow their history beyond this point.

¹ Since the chemical nature of this body is not known it has been thought better to apply a descriptive term to it, rather than to call it a nucleolus, karyosome, or chromosome vesicle, each of which it resembles in certain respects.

THE MATURATION DIVISIONS.

No special interest attaches to these and they will be passed over rapidly. The first division is reductional for autosomes and X-chromosome. The former appear as dyads with little evidence of a tetrad structure. Such a structure probably exists, however, and further extraction would perhaps bring it out, for in early anaphase each component of the dyad is itself clearly double. The X-chromosome goes to one pole in the first division and divides in the second. Metaphases of the first division and of the two types of second division are shown in Figs. 14 to 16.

OÖGENESIS.

Knowing the unusual behavior of the chromosomes during spermatogenesis, it would be of especial interest to determine whether or not similar phenomena occurred during oögenesis, but this has proved to be a very difficult task. Owing to the nature of oögenesis only a few, rather widely separated stages can be found in any one ovary, and the story has to be pieced together from an examination of many specimens. The orientation of stages, especially the early ones, is very difficult. Consequently I am only able to record a few observations at this time.

The chromosome group of the female, as expected, consists of five pairs—differing from that of the male only in the presence of two X-chromosomes instead of one (Fig. 22).

Near the apex of the ovarian tubules, in the region of transition from oögonia to oöcytes and nurse cells, are found nuclei with chromosomes such as those represented in Fig. 23 (probably oögonial) and in Figs. 24 to 28. In the latter very obvious loops are present, bearing a strong resemblance to those in the spermatocytes. These chromosomes are not pulling apart on the spindle, as their outlines might suggest, but are in resting nuclei, or at least nuclei that are not actively preparing to divide. Whether they represent the final generation of undifferentiated ovarian cells or represent an early growth stage of oöcytes and nurse cells, I am unable to determine. If the latter, then they may correspond to spermatocytes in the aggregated stage *b*. In any case, the condition seems to parallel that found in the male, for I have not

observed such loop structures in any other Diptera. This gives some ground for expecting similar synaptic phenomena in the two sexes in regard to the feature with which we are concerned here.

After the growth period is well under way and the oöcytes are clearly differentiated from the other cells, the chromatin appears in the form of large, irregular, heavily granulated aggregates whose structure I am unable to analyze. Before this, however, there appears to be a diffuse stage in which scarcely any chromatin is visible in the nucleus. My present material is not adequate for a detailed study of these stages and their treatment must be deferred.

DISCUSSION.

The above facts, it is believed, provide strong support for the conclusion that, in the male *Dasyllis* at least, synapsis is not uniform throughout the length of the chromosomes, but may, in the case of certain chromosomes, occur only in the terminal regions, leaving the homologous members separated near the middle.

So far as I know, no equally clear cases of this sort have been described before, although figures that suggest a similar condition are given by Mohr ('16, Figs. 85-90) for *Locusta viridissima*, by Robertson ('16, Fig. 163) for *Chortippus curtipennis*,² and by Wenrich ('16, Figs. 73-78) for *Phrynotettix magnus*. These are interpreted by the authors as cases of delayed synapsis (*Locusta* and *Phrynotettix*), or early separation of threads after synapsis (*Chortippus*); but it is possible that with further study some of them may prove to be cases of incomplete synapsis. Professor McClung informs me that similar conditions may exist in other Orthoptera on which he has made preliminary observations.

It has also been suggested to me by McClung that the absence of synapsis in the median part of the long J- and V-shaped chromosomes in *Dasyllis* may be due to these chromosomes each being compounded of two rod-like chromosomes united end to end, as he has found chromosomes to be united in *Hesperotettix* (McClung, '17). This offers an attractive lead toward an explanation, but it is necessary to assume some other influence as well, else all compound chromosomes should show this behavior. The latter

²I am indebted to Prof. E. B. Wilson for calling my attention to the former, and to Prof. C. E. McClung for calling my attention to the latter case.

influence seems to lie deeper in the chromosome organization. It is not revealed, however, by any morphological feature such as a difference in length or structure of the two components of a loop. Genetically one might assume the presence of balanced lethals to account for the results; but there is no evidence of their being present, and no chance of securing such evidence, because the flies are unsuitable for genetical study.

It is to be noted that the looped region of the chromosomes in *Dasyllis* is usually median. In many organisms the middle of the chromosome is apparently the last part to undergo synapsis, which suggests that the process in *Dasyllis* is actually an incomplete but otherwise normal synapsis. On the other hand, in the Diptera thus far studied, the synaptic process appears to be very different from that in other organisms, and there is no indication of synapsis beginning at the ends of the chromosomes and progressing toward the middle. Nevertheless, the fact that three pairs of chromosomes are affected similarly suggests an influence on the general synaptic process in these organisms, rather than the independent action of agents located in the respective pairs.

The chromosome behavior in *Dasyllis* recalls the genetical behavior of certain strains of *Drosophila melanogaster* in which crossing-over is greatly diminished in certain parts of linkage groups (Muller, '16; Sturtevant, '19; Detlefsen, '20). This decrease or elimination of crossing-over in part of a chromosome is just what one would expect from an incomplete synapsis such as described above.

However, it will be necessary to get both the genetical and cytological data from one organism before the evidence becomes satisfactory, and I do not wish to push the present analogy. In *Drosophila* crossing-over occurs only in the female. If this is true in *Dasyllis*, then oögenesis rather than spermatogenesis must be used for comparison. It also appears from the *Drosophila* data that many, if not most, of the cross-over modifications manifest themselves only in flies heterozygous for the cross-over "genes." In other words, as Sturtevant has suggested (p. 329), they appear to be due to an unlikeness in homologous chromosomes. In *Dasyllis* there is at present no evidence that the homologous chromosomes differ in the regions where synapsis fails to occur.

The cases involving different cross-over values in homozygous strains of *Drosophila* (C^m of Sturtevant, and unpublished data kindly furnished by Dr. Bridges) provide a closer analogy. At present it can only be said that the chromosome behavior in *Dasyllis* illustrates a type of mechanism which should give results similar to those observed in *Drosophila*.

LITERATURE CITED.

Carothers, E. E.

- '13 The Mendelian Ratio in Relation to Certain Orthopteran Chromosomes. Journ. Morph., 24: 487-511.

Detlefsen, J. A.

- '20 Is Crossing Over a Function of Distance? Proc. Nat. Acad. Sciences, 6: 663-673.

McClung, C. E.

- '17 The Multiple Chromosomes of *Hesperotettix* and *Mermiria* (Orthoptera). Journ. Morph., 29: 519-605.

Metz, C. W.

- '16 Chromosome Studies on the Diptera. II. The Paired Association of Chromosomes in the Diptera, and its Significance. Journ. Exp. Zool., 21: 213-279.

Metz, C. W., and José F. Nonidez.

- '21 Spermatogenesis in the Fly, *Asilus sericeus* Say. Journ. Exp. Zool., 32: 165-185.

Mohr, Otto L.

- '16 Studien über die Chromatinreifung der männlichen Geschlechtszellen bei *Locusta viridissima*. Liège, H. Vaillant-Carmanne (Société Anonyme). 176 p.

Muller, H. J.

- '16 The Mechanism of Crossing Over. Amer. Nat., 50: 193-434.

Robertson, W. R. B.

- '16 Chromosome Studies. I. Taxonomic Relationships Shown in the Chromosomes of Tettigidae and Acrididae: V-shaped Chromosomes and their Significance in Acrididae, Locustidae, and Gryllidae: Chromosomes and Variation. Journ. Morph., 27: 179-331.

Sturtevant, A. H.

- '19 Inherited Linkage Variations in the Second Chromosome. Contributions to the Genetics of *Drosophila melanogaster*, Carn. Inst. of Wash. Pub. No. 278: 305-342.

Wenrich, D. H.

- '16 Spermatogenesis of *Phrynotettix magnus* with Special Reference to Synapsis and the Individuality of the Chromosomes. Bull. Museum Comp. Zool. Harvard, LX.: 57-133.

EXPLANATION OF PLATES.

All figures were drawn from sections 5μ in thickness, with the aid of a camera lucida. Magnification approximately 3,000 diameters.

PLATE I.

All figures except numbers 1 and 2 are from *Dasyllis grossa*; numbers 1 and 2 are from specimens not yet identified as to species.

FIG. 1. Spermatogonial metaphase.

FIGS. 2 and 3. Spermatogonial prophase.

FIG. 4. Very early growth stage, only one aggregate or chromosome pair represented.

FIG. 5. Same stage, representing portion of another aggregate.

FIG. 6. About the same, or slightly later stage, showing two aggregates.

FIG. 7. Slightly later stage after the chromosomes have moved to periphery of nucleus. One chromosome pair and attached dense body represented.

FIGS. 8 TO 10. Similar stages showing other chromosomes. The chromosome pair on the left in Fig. 9 is presumably the small pair which usually has no loop or a very small one.

FIG. 11. Later stage, about middle of growth period. Entire nucleus represented, including the four pairs of autosomes and the small, condensed X.

FIG. 12. Later stage, entire nucleus; chromosomes transposed to facilitate examination.

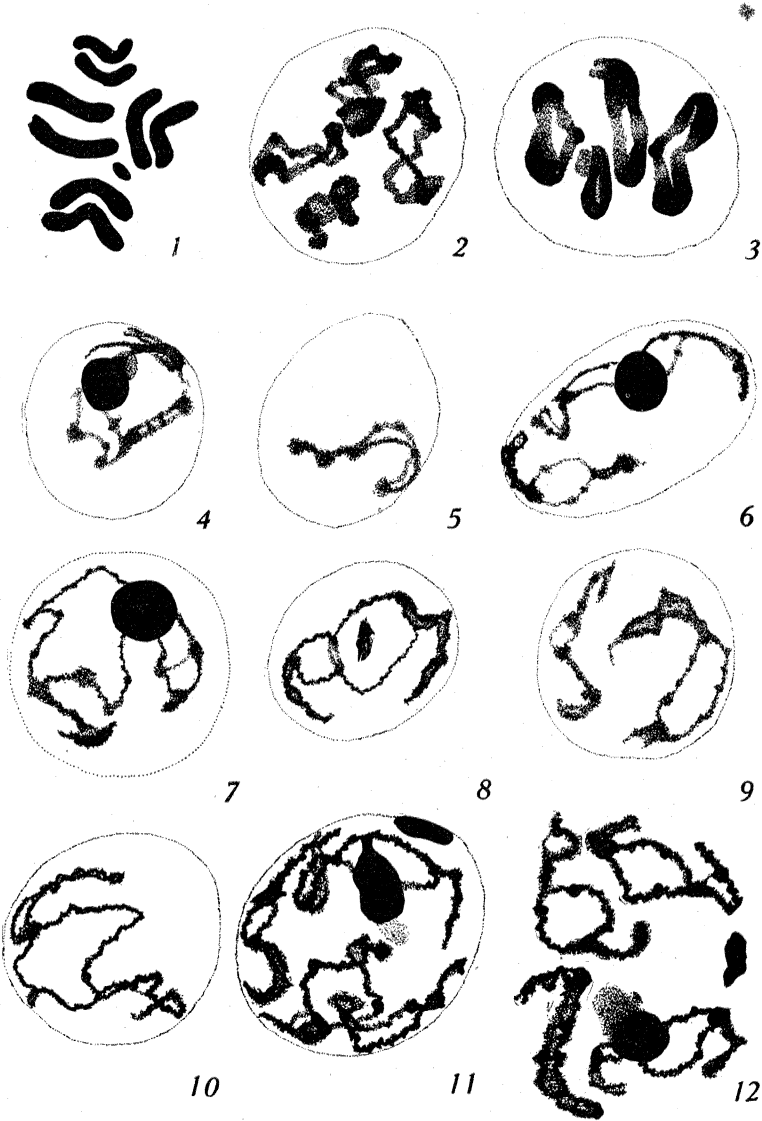


PLATE 2.

FIGS. 13 TO 21. ♂ *Dasyllis grossa*; Figs. 22 TO 28 ♀ *Dasyllis*, species not yet determined.

FIG. 13. Late prophase, first spermatocyte.

FIG. 14. Metaphase, first spermatocyte.

FIGS. 15 AND 16. Metaphases, two types of second spermatocytes, the former with X., the latter without it.

FIGS. 17 TO 19. Examples of the rare cases in which the dense body is represented by two separate smaller bodies.

FIGS. 20 AND 21. Examples of the chromosome pair with dense body attached, in late prophase.

FIG. 22. Ovarian cell (oögonium?), prophase showing loose association of middle region of large chromosomes.

FIGS. 24 TO 28. Chromosomes from oögonia, or early growth stage of oöcytes or nurse cells, showing median loops resembling those in the male.

